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Native range size and growth form in Cactaceae predict invasiveness and impact

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Abstract

Many recent studies in invasion science have identified species traits that determine either invasiveness or impact. Such analyses underpin risk assessments and attempts to prioritise management actions. However, the factors that mediate the capacity of an introduced species to establish and spread (i.e. its invasiveness) can differ from those that affect the nature and severity of impacts. Here we compare those traits correlated with invasiveness with those correlated with impact for Cactaceae ("cacti") in South Africa.

To assess impact magnitude, we scored 70 cacti (35 invasive and 35 non-invasive species) using the Generic Impact Scoring System (GISS) and identified traits correlated with impact using a decision tree approach. We then compared the traits correlated with impact with those identified in a recent study as correlated with invasiveness (i.e. native range size and growth form).

We found that there is a significant correlation between native range size and both invasiveness and impact. Cacti with larger native ranges were more likely to become invasive ($p=0.001$) and cause substantial impacts ($p=0.01$). These results are important for prioritising efforts on the management of cactus species. Understanding when and why impact and invasiveness are correlated (as they appear to be for Cactaceae) is likely to be an important area of future research in risk assessment.

Keywords

Biological invasions, invasibility, invasiveness, risk assessment, spread, weediness

Introduction

Humans have moved species to areas outside their native ranges for millennia, and alien species are now common components of most ecosystems (van Kleunen et al. 2015). Although only a small proportion of introduced organisms establish and spread in new areas, alien species can cause significant negative environmental and socioeconomic impacts (Richardson 2011, Simberloff and Rejmánek 2011). These include loss of biodiversity (Powell et al. 2013), changes to ecosystem functioning (D'Antonio and Vitousek 1992), large economic losses (Pimentel et al. 2000, Pimentel et al. 2005, Holmes et al. 2009) and impacts on human health (Hulme 2014). To minimize such negative impacts, strategies for managing alien species have been developed in many parts of the world (Pyšek and Richardson 2010). Given the high economic, cultural or aesthetic value ascribed to many alien species and the limited availability of resources to manage their negative impacts (Hester et al. 2013), a key challenge for managers is to identify future invaders and those alien species that are likely to cause the most damage.

In this study we define invasive species in a strictly biogeographic sense (sensu Richardson et al. 2011); this definition excludes connotations relating to impact. This is in contrast to the definition often used by policy makers, especially in Europe and North America, where invasive species are defined as those alien species that have negative impacts. Much work has recently focussed on identifying potentially invasive species. For example, several studies have compared known invasive and non-invasive alien species within particular taxonomic groups searching for traits associated with invasion success (Rejmánek and Richardson 1996, Pyšek and Richardson 2007, Küster et al. 2008, van Kleunen et al. 2010). Studies following this approach typically identify alien species with certain reproductive traits, growth forms, physiology, or characteristics of their native ranges as species with a high likelihood of becoming invasive (e.g. Muth and Pigliucci 2006, Feng et al. 2008, van Kleunen et al. 2010, Castro-Díez et al. 2011, Gallagher et al. 2011, Novoa et al. 2014).

Although this approach has been reasonably successful in identifying likely invaders, species thus flagged are not necessarily those likely to cause the most damage – invasiveness often does not correlate with impact (Ricciardi and Cohen 2007). The traits that influence invasiveness (the capacity to establish and spread) are different to those that determine impact (the capacity to alter features of invaded ecosystems or the services they deliver). Although the magnitude of impacts is a function of how abundant and widespread a species is (Parker 1999), an alien species with limited distribution can still have greater impacts than an abundant widespread invader. However, traits for invasiveness and impact are usually assessed either separately, or together, but without clearly separating which traits affect invasiveness and which affect impacts (e.g. Pheloung et al. 1999). Strategies for managing alien species require an understanding of both sets of traits, and in particular how they overlap. For example, species in a particular taxonomic group of plants might be much more likely to become invasive if they have small seeds (they are easily dispersed), while in the same group of species those with high pollen production cause the greatest impacts (by causing hay fever).

If pollen production and seed size are independent traits, then we need to prioritise management efforts against taxa with both small seeds and high pollen production. An additional complication is that effects can be in different directions, e.g. a trait might increase the chance of a species being introduced but reduce the chance of an introduced species becoming invasive (Moodley et al. 2013).

Progress has, however, been made in terms of categorising and comparing the wide variety of mechanisms by which an introduced species can cause negative impacts (Blackburn et al. 2014). To identify species traits associated with impact to inform alien species management, Nentwig and colleagues (2010) developed a Generic Impact Scoring System (GISS) [subsequently extended by Kumschick and Nentwig (2010) and Kumschick and colleagues (2012) and modified by Blackburn and colleagues (2014)] which allows for comparison of the magnitude of impact between species and taxonomic groups. The GISS has proven useful for comparing the impact of alien birds, mammals, fish, arthropods and plants in Europe (Nentwig et al. 2010, Kumschick and Nentwig 2010; Kumschick et al. 2012, Kumschick et al. 2015), and the impact of birds in Australia (Evans et al. 2014).

We use the family Cactaceae in South Africa as a case study to assess how traits related to invasion success differ from traits related to impact. Thirty-five of the approximately 250 cacti species that have been introduced to South Africa are currently recorded as invasive (Novoa et al. 2015). The impacts of cactus invasions on South African biodiversity, resource availability, national economy, and human health have been recognized for well over a century (e.g. Walters et al. 2011). Consequently, a broad assessment of the determinants of invasiveness and impacts of the family Cactaceae in South Africa is an important requirement for the formulation of a national strategy for the management of alien cactus species.

Novoa and colleagues (2014) looked at invasive and non-invasive species within the family Cactaceae and found that invasive species tended to have larger native range sizes, come from certain genera (especially *Opuntia*), and have certain growth forms (cylindrical, flattened-padded, sprawling, leaf-like or angled in particular). In this study, we applied the GISS to assess and compare impacts of cacti in South Africa and other non-native ranges, and analysed the results to identify species traits correlated with the magnitude of the impacts. Finally, we compare the traits associated with species invasiveness in South Africa with those associated with negative impacts outside their native range, and make recommendations for the management of current and future cactus invasions.

Cactaceae ("cacti") is a family of 1919 species, with all but one species native to the Americas (Novoa et al. 2014). Cacti have been moved to regions outside their native ranges mainly as ornamental species (Walters et al. 2011) since the fifteenth century (Howard and Touw 1981). Some cactus species have become invasive and are among the most damaging invasive species worldwide (Weber 2003), with hotspots of invasion in Australia, South Africa, and Spain (Novoa et al. 2014). We focus on the invasion of cacti in South Africa, the region for which the history of introductions and impact of cactus species is best documented.

Methods

Species selection

The first alien cactus species (*Opuntia ficus-indica*) was introduced to South Africa in the 18th century (Annecke and Moran 1978). Since then, many more species have been introduced for ornamental purposes (Walters et al. 2011). We recently surveyed the ornamental trade of Cactaceae in South Africa. The six main wholesale nurseries supplying cacti predominately produce plants for sale directly from imported seed. Records of seed importation therefore provide a reliable estimate of propagule pressure. We selected 70 cactus species introduced to South Africa: the 35 cactus species currently listed as invasive under South African national regulations (Novoa et al. 2015), and the 35 non-invasive cactus species which are most prominent in the ornamental trade, as determined by numbers of seeds imported (Novoa et al. unpubl. data).

For each species, we searched the ISI Web of Knowledge and internet (using Google and Google Scholar) for publications and datasets. From the data collated we determined: the taxonomic identity, dispersal potential of each species [vegetative growth (yes/no), fleshy/edible fruits (yes/no), growth form (drawn from Novoa et al. 2014)], maximum height, native range size (in latitudinal degrees; Novoa et al. 2014), and the presence of spines (yes/no) (Table 1 and Suppl. material 1).

Impact assessment

To compile information on the impacts of the 70 species, we searched the ISI Web of Knowledge and internet (using Google Scholar) for publications, websites, datasets, and grey literature on the negative impacts of cactus species outside their native ranges (see Suppl. material 2). We did this using the scientific and common species names as search terms, and screening the titles and abstracts of the resulting papers and those papers cited in their reference lists. All the sources of information were given equal weight; by using the *maximum* impacts reported we employ a precautionary approach. Often the only evidence of impact was reported in the grey literature and on websites.

The GISS used for this study considers 12 impact categories divided into two main groups. The first group consists of environmental impacts, including impacts (1) on vegetation, (2) on animals, (3) through competition, (4) through transmission of diseases or parasites to native species, (5) though hybridization and (6) on ecosystems. The second group deals with socioeconomic impacts, on (7) agriculture, (8) animal production, (9) forestry, (10) human health, (11) human infrastructure and administration, and (12) human social life. Within these 12 categories, impact is assessed using a semi-quantitative scale (Kumschick et al. 2015), with six impact levels ranging from zero (no impact known or no data available) to five (highest impact possible at a site). The impact levels in each category are described verbally with scenarios to assure

Table 1. Species traits here considered as potentially responsible for the maximum recorded impact scores according to GISS.

Trait	Description	Justification	Reference
Native range size	Due to a lack of distribution data, we measured the native range size in latitudinal ranges, translated from the information on the native range of cactus species described in Anderson (2001)	More widely distributed species are more likely to be transported, disseminated, and have impacts in new habitats	Moodley et al. 2013
Height	Maximum plant height measured in meters sensu Anderson (2001)	Pyšek and colleagues suggested that taller plants might be more likely to exert a significant impact than shorter plants	Pyšek et al. 2012
Fleshy fruits	Yes/no	Most fruits of cactus species are spiny. Fleshy fruits are more likely to be consumed by animals and humans. Cactus species with fleshy fruits are more likely to cause impacts through injuries caused by spines.	Anderson 2001
Spineless (or small spines)	Yes/no	Cactus spines can cause injuries with clinical significance	Lindsey and Lindsey 1988
Vegetative growth	Yes/no	Cactus species with detachable vegetative propagules are likely to cause severe injuries to humans and animals	Walters et al. 2011
Growth form	Angled, cylindrical, cushion-like, leaf-like, flattened-padded, geophytic, globose, ovoid, sprawling, tree-like, tuberculate and prostrate (sensu Novoa et al. 2014). Sensu Novoa et al (2014)	Growth form has been shown to be correlated with invasiveness. We test whether impact is also correlated with growth form. Reasons could be that different growth forms offer different capacities to grow vegetatively from cuttings, and vegetative propagules are likely to cause severe injuries to humans and animals	Novoa et al. 2014; Walters et al. 2011

consistency between assessors. All impact records found in the literature were assigned an impact level accordingly. The highest scores found per species, category and group (environmental and socioeconomic) were used for the analysis. More detail on the GISS can be found in Kumschick and Nentwig (2010), Kumschick et al. (2012) and Kumschick et al. (2015).

Following Kumschick et al. (2015), we assigned all impact records found in the literature to a category and score them. As suggested by Blackburn et al. (2014), we used the *maximum* impact over all categories as a measure of magnitude of impact. We calculated each measure for impacts in South Africa only and impacts through the entire introduced range, including South Africa (to also assess the potential impact of those species introduced to South Africa but with no known impact yet). For each species, we calculated each of these measures for environmental impact and socioeconomic impact separately (including six categories each). This led to four measures: (i) maximum environmental impact; (ii) maximum socioeconomic impact; (iii) maximum environmental impact in South Africa; and (iv) maximum socioeconomic impact in South Africa.

Finally, we conducted a decision-tree analysis using the rpart package (Therneau et al. 2009) included in the Rattle package (Williams 2009) in R (version 3.0.2) to identify which species traits are associated with the observed maximum impact scores. We also conducted a t-test in R to explore the differences in native range size between non-invasive and invasive species, and an ordinal logistic regression to study the correlation between the native range size and the impact scores.

Results

Impact assessment

Despite their long history of introduction around the world, as expected, we found no evidence of impacts for the 35 cactus species considered as non-invasive in South Africa (Suppl. material 4). Among the 35 invasive species, *Opuntia aurantiaca* Lindl., *O. ficus-indica* and *O. pubescens* H.Wendl. ex Pfeiff. had the highest scores for impact in most categories, but *O. stricta* (Haw.) showed the highest impact scores in the overall environmental category.

We found no evidence of impacts of any cactus species through the transmission of diseases or parasites or through hybridization outside their native range. Moreover, in South Africa we found no evidence of impacts on ecosystems (e.g. chemical, physical or structural changes) or social life (Table 2). Overall, impacts on animals and animal production were the most important environmental and socioeconomic impacts respectively due to the spines of cactus species causing serious injury to native animals and livestock.

Of the six traits analysed (Table 1), native range size consistently emerged as the main trait associated with the observed impact scores. Species with large ranges tended to have larger impacts. The decision tree for environmental impact in South Africa identified two splits, both due to range size: large ranges with many impacts vs. smaller

Table 2. Maximum environmental and socioeconomic impacts of invasive cacti (n= 35) in South Africa and over the entire non-native range. The impact scores are based on the Generic Impact Scoring System (GISS) and range from 0–5. No invasive cacti had no recorded impacts.

	Categories	South Africa	Whole non-native range
Maximum environmental impacts	On vegetation	3	3
	On animals	4	4
	Through competition	3	3
	Transmission of diseases or parasites to native species	0	0
	Through hybridization	0	0
	On ecosystems	0	3
Maximum socioeconomic impacts	On agriculture	3	3
	On animal production	5	5
	On forestry	3	3
	On human health	1	2
	On human infrastructure and administration	2	3
	On human social life	0	4

ranges with fewer impacts; and secondly small ranges with no or few impacts vs. medium ranges with some impacts (Figure 1). This relationship is probably log-linear (Figure 2). We also found a relation between native range size and invasiveness (Figure 3) and maximum environmental and socioeconomic impact of cacti in South Africa and over the whole non-native range (Figure 2). Additionally, species with flattened cladodes had the highest socioeconomic impacts over the entire non-native range.

Discussion

Our results suggest that native range size of species in the family Cactaceae is correlated with both invasiveness ($p<0.001$, Figure 3) and impact ($p=0.01$, Figure 2). Many studies have shown positive relationship between native range size and invasiveness (e.g. Duncan et al. 2001, Forsyth et al. 2004, Shah et al. 2012, Allen et al. 2013, Bates et al. 2013). One potential explanation is that widespread species are more likely to be encountered and introduced to other regions (Pyšek and Richardson 2008). However, as we indicated before, this is not true for cactus species. From records of seed imports of the last 50 years (Novoa et al. unpublished data) it is clear that the non-invasive species considered here have been widely cultivated in South Africa. Indeed, these species are likely to have had a greater propagule pressure from horticulture than the invasive species. For example, approximately 8 million seeds of *Echinocactus grusonii* have been brought to South Africa since the 1960s. By contrast, only 636 000 seeds of

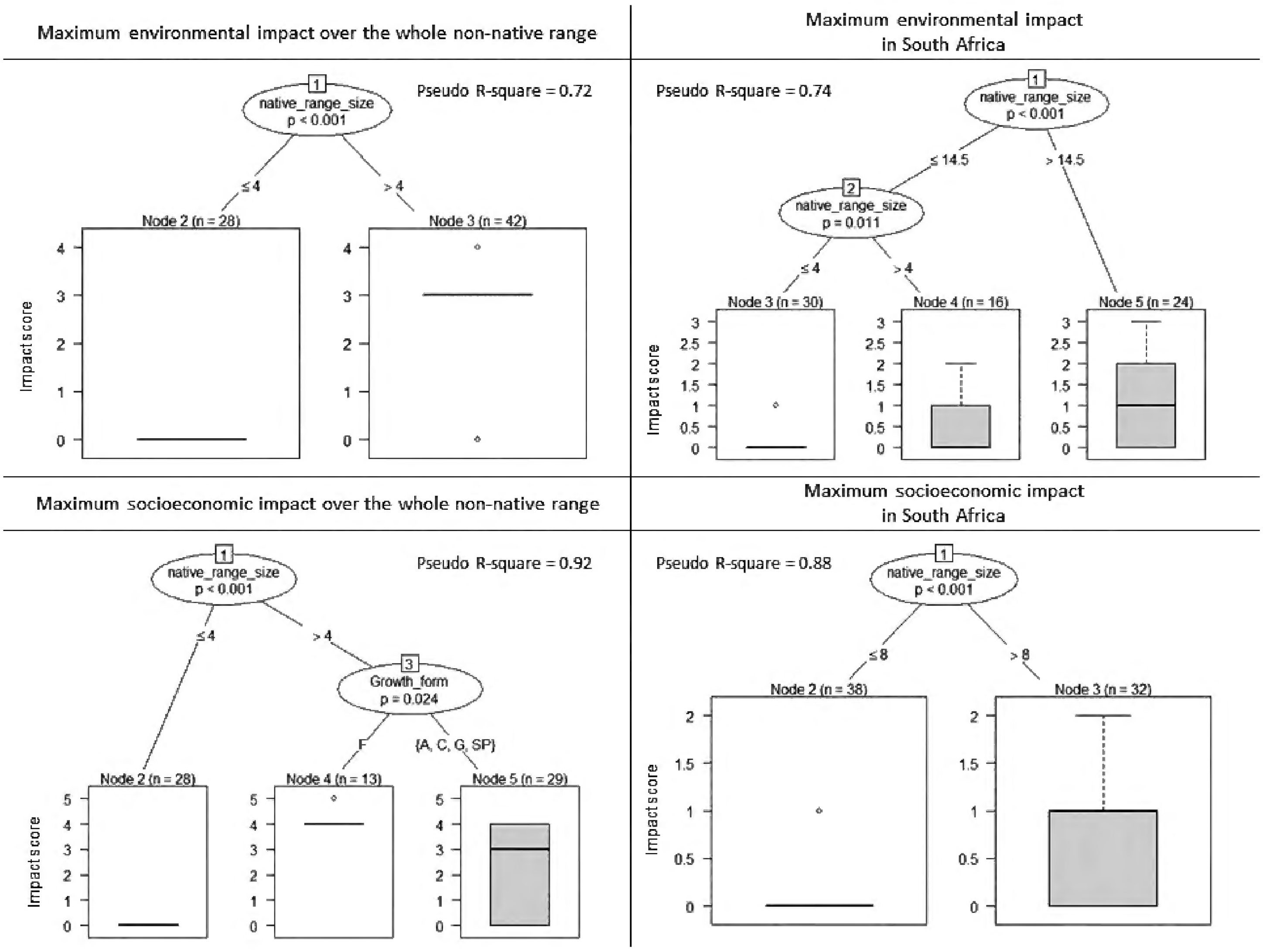

Figure 1. Conditional decision tree identifying the cactus traits responsible for the scores obtained from the Generic Impact Scoring System. Growth forms: A = Angled, C = Cylindrical, F = Flattened-padded, G = Globose, SP = Sprawling. Native range size is expressed in latitudinal degrees.

Cereus hildmannianus have been introduced over the same period. Both species have only been used for horticulture but *C. hildmannianus* is invasive and *E. grusonii* is not. The native range of *C. hildmannianus* is, however, about forty times that of *E. grusonii*.

Several studies have argued that species with large native ranges possess a suite of traits that contribute to fitness and dispersal (Booth et al. 2003), and have wide environmental tolerances which improves their ability to handle different conditions in new areas (Allen et al. 2013, Lavoie et al. 2013). We believe that this is especially true for the family Cactaceae, one of the families with the highest number of endangered species in the plant kingdom (Hernandez and Barcenas 1996, Goettsch et al 2015). Most cacti (especially those with a globose growth form and therefore limited dispersal rates) have small native ranges and need specific climatic and environmental conditions to germinate, grow and spread (Anderson 2001, Godínez-Álvarez et al. 2003, Drezner and Lazarus 2008). It is therefore not surprising that only those cactus species that are able to establish and spread under a variety of conditions (and therefore become widespread in their native range) are able to successfully establish and become invasive when introduced to new regions.

Moreover, Novoa and colleagues (2015) found that species in certain genera (*Austrocylindropuntia*, *Cylindropuntia*, *Harrisia*, *Hylocereus* and *Opuntia*) and with certain

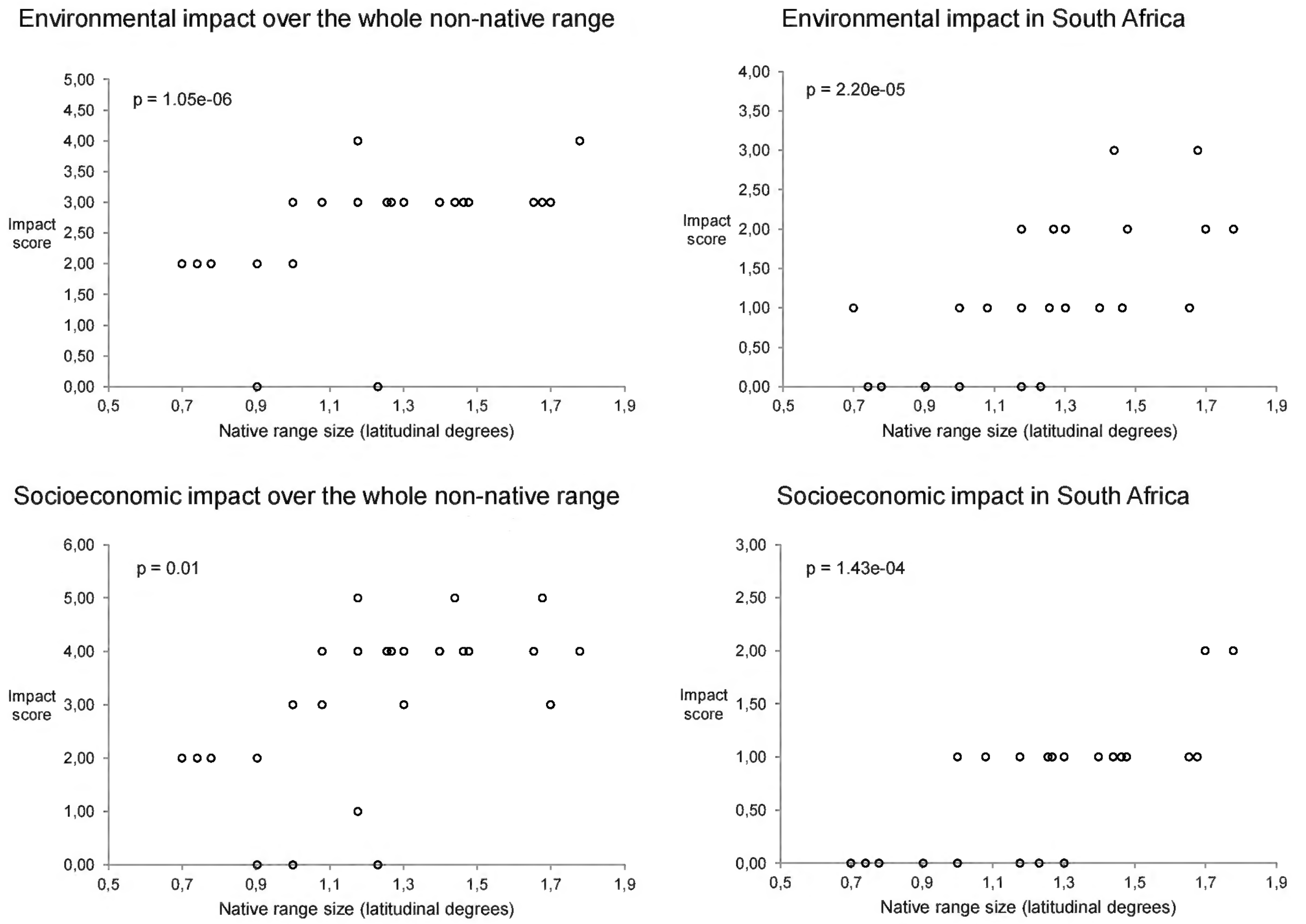

Figure 2. Relationship between native range size and maximum impact. Invasive species with larger native ranges have significantly greater impact. Native range size is expressed in latitudinal degrees and plotted on a logarithmic scale. Impact scores were obtained from the Generic Impact Scoring System (max of 5).

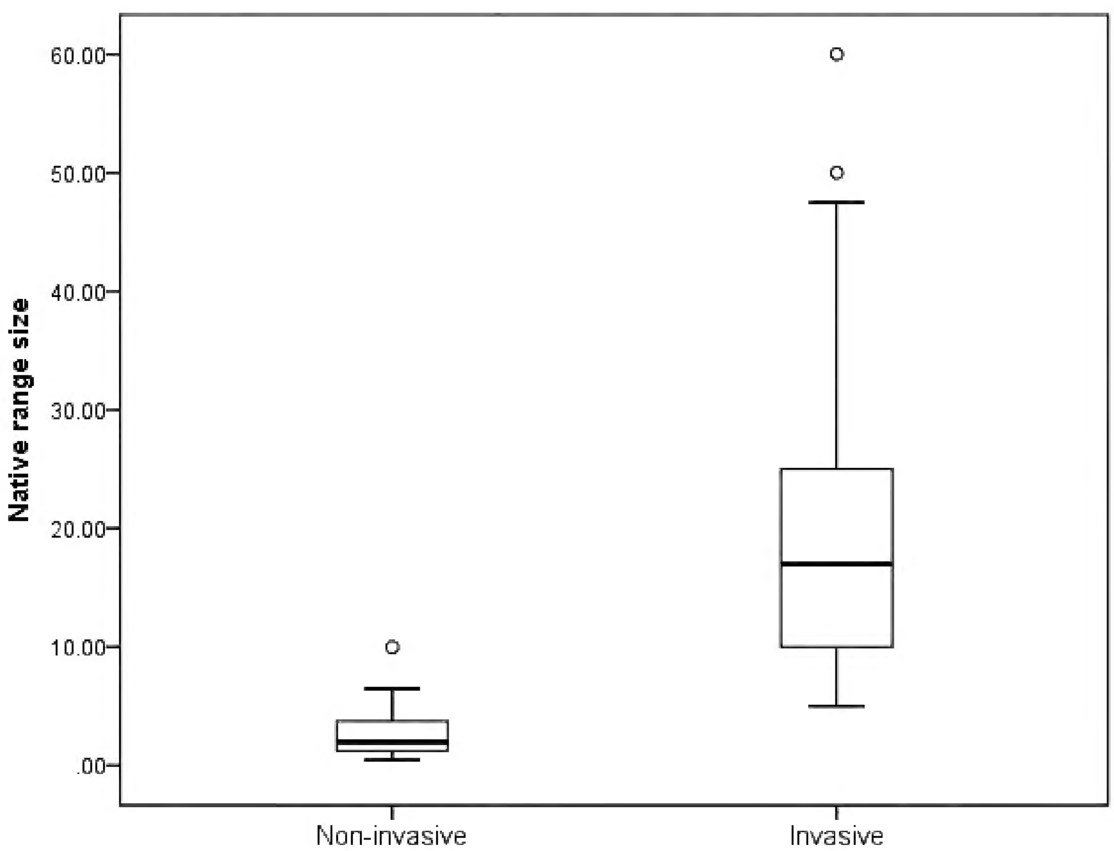

Figure 3. Relationship between native range size and invasiveness. Of the 70 cactus species introduced to South Africa explored here, invasive species have significantly ($p<0.001$) larger native range sizes than non-invasive species. Native range size is expressed in latitudinal degrees.

growth forms (flattened-padded and angled) are also likely to become invasive, and that growth form plays a role in socioeconomic impacts (species with a flattened-padded growth form showed the highest socioeconomic impacts). Consequently, risk assessment protocols for cacti should consider not just native range sizes but should also evaluate taxa according to genera and growth forms. In addition, the cactus species with the greatest impacts outside their native ranges (especially socioeconomic impacts) were *Opuntia* species which are the most common invasive cacti (Novoa et al. 2014). Therefore, management of taxa in this genus should be a top priority. Fortunately for the management of cacti, *Opuntia* species are probably the most easily identified of all cactus species (Lloyd and Reeves 2014) due to their distinct flattened-cladode growth form (Novoa et al. 2014).

Our results also suggest that the highest negative impacts of cactus species are those related to animal production. Cactus invasions cause injuries to livestock, contaminate wool and prevent access to grazing land (e.g. Walters et al. 2011, Lloyd and Reeves 2014). Therefore, areas where livestock farming is important should be prioritized when managing cactus invasions. This is especially important for South Africa, since 69 % of South Africa's land surface is suitable for grazing, and livestock farming is the largest agricultural sector in the country (Goldblatt 2010).

Although South Africa is the region where the introduction and impact history of cactus species is best documented (e.g. Walters et al. 2011) studies on this topic are still scarce and it is likely that not all negative impacts of cacti have been detected and recorded yet. For example, although some studies in South Africa mentioned that invasive cacti might have potential impacts on ecosystem functioning (e.g. Walters et al. 2001), this remains to be conclusively demonstrated. There are no documented examples of impacts on ecosystems or social life. Such a lack of knowledge is, however, a common problem when assessing risks associated with alien species (Hulme et al. 2013).

While the correlation between native range size, invasiveness, and impact observed here is a useful starting point for prioritising cactus management, more work is required to understand the underlying mechanisms. Does the dispersal capacity of different cactus species influence native range size and both invasiveness and impact? How would this relate to environmental (e.g. impacts on ecosystem functioning), economic (e.g. economic losses in animal production) and social (e.g. impacts on social life) consequences of cactus invasions? While we are not able to address all these questions here, we believe that analyses that explicitly examine both invasiveness and impact offer an opportunity to further both our theoretical understanding of invasions and how we manage them in practice.

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Supplementary material 1

Selected species and traits

Authors: Ana Novoa, Sabrina Kumschick, David M. Richardson, Mathieu Rouget, John R. U. Wilson

Data type: multimedia

Explanation note: NA = No information available.

Supplementary material 2

List of the sources of information used for the impact scoring according to GISS

Authors: Ana Novoa, Sabrina Kumschick, David M. Richardson, Mathieu Rouget, John R. U. Wilson

Data type: bibliography

Supplementary material 3

Generic Impact Scoring System (GISS)

Authors: Ana Novoa, Sabrina Kumschick, David M. Richardson, Mathieu Rouget, John R. U. Wilson

Data type: multimedia

Explanation note: Detailed description of impact categories. An updated Excel version is available from the authors on request.

Supplementary material 4

Results of the General Impact Scoring System applied to 70 cactus species (35 invasive and 35 non-invasive cactus species with a long history of introduction in South Africa)

Authors: Ana Novoa, Sabrina Kumschick, David M. Richardson, Mathieu Rouget, John R. U. Wilson

Data type: measurement

Explanation note: The impact scores are expressed as the maximum impact over all the environmental and socioeconomic categories considered in this study.